

The Mechanical Behavior of the Human Forearm in Response to Transient Perturbations

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Abstract. Static and dynamic components of mechanical impedance of human forearm were evaluated by applying two kinds of perturbations: 1) large viscoelastic loads, and 2) small pseudo-random perturbations. When the task involved the active resistance of the perturbations, both stiffness and viscosity increased relatively to their values in the passive task, the increment in stiffness being larger than that in viscosity. The time course of such changes was investigated during the transition between the two operating points defined by the instructions “do not resist” and “resist” the applied perturbations. The changes in stiffness and viscosity were relatively slow, those in the latter lagging behind those in the former.

Introduction

A limb whose position has been externally perturbed develops restoring forces which result from the intrinsic viscoelastic properties of muscles, from reflex mechanisms, and from a possible voluntary intervention (cf. Matthews, 1972; Stein, 1974; Houk, 1978; Terzuolo et al., 1981). One way of characterizing the global ability of the system to deal with perturbations is to evaluate its output impedance, defined as the ratio of the limb angular displacement to the applied torque disturbance. Mechanical impedance has both static and dynamic components: the former corresponds to stiffness, the latter to viscosity. Common experience tells us that different behavioral situations may impose different requirements upon the limb control properties and, consequently, may demand variable degrees of stiffness and/or viscosity. In fact, several studies have shown that the steady-state values of both parameters are indeed variable and depend on the specific operating point. For example, they are a function of

the amplitude and frequency of the perturbations (Viviani and Terzuolo, 1973; Joyce et al., 1974; Viviani and Berthoz, 1975), of the mean muscular tension (Wilkie, 1950; Stark, 1968; Rosenthal et al., 1970; Agarwal and Gottlieb, 1977; Zahalak and Heyman, 1979), and of the joint angle (Dufresne et al., 1978; Gottlieb and Agarwal, 1978). Also the instruction given the subject affects output impedance (Stark, 1968; Wieneke and Denier van der Gon, 1974; Dufresne et al., 1978), even though it is difficult to assess its influence independently of concomitant changes in other variables (for instance, the level of muscular contraction).

In this paper we shall present results concerning the characteristics of the forearm transient responses associated with the instructions “do not resist” and “resist” the perturbations. The effects of disturbances of a very different nature and amplitude were compared by performing two series of experiments. In the first, the angular position at the elbow was perturbed by large viscoelastic loads generated by a pair of springs attached to the forearm in a push-pull fashion. The resulting underdamped oscillations of the forearm allowed a quick evaluation of its mechanical parameters and a check of non-stationarities in the system. In the second experimental series, the applied perturbations consisted of pseudo-random torque pulses (Dufresne et al., 1978), which are small, unpredictable signals interfering minimally with the execution of a motor task (Dufresne et al., 1980; Soechting et al., 1981). The other advantage associated with the use of random inputs is that the range of linearity of the system is extended compared with that observed using other kinds of inputs (Agarwal and Gottlieb, 1977; Dufresne et al., 1978). In this second series of experiments we applied a recently developed identification technique which provides a quasi-continuous description of non-stationary systems (Soechting et al., 1981) in order to examine the temporal evolution of the

impedance in the transition from the state specified by the instruction not to resist the perturbations to the state specified by the instruction to resist them. Indeed, in contrast with the wealth of data on steady-state values of output impedance, not much is known about the time course of their changes in the transition from one operating point to another. How fast are these changes? Do static and dynamic stiffness have the same or different time courses? How do their time courses compare with those of changes in muscular activity and in the amplitude of reflex responses? Data pertinent to these questions will be presented and discussed.

Methods

Experimental Set-Up

Seven subjects participated in this study. They were seated with their right forearm clamped to a light-weight lever system. In the experiments involving viscoelastic loading, the distal extremity of the lever was attached to a pair of springs arranged in a push-pull fashion. The springs were therefore in parallel with biceps and triceps, and they were in equilibrium when the forearm-lever system was in a horizontal position. The forearm-lever complex was set to an initial position of about 110° elbow extension from which it was abruptly released and made oscillate driven by the springs. Three pairs of springs of different stiffness were used; they will be designated as "weak" (stiffness $k=24$ kg/m), "medium" ($k=34$ kg/m), and "stiff" ($k=190$ kg/m).

In the experiments involving pseudo-random perturbations, the forearm-lever complex was coupled to a torque motor with the elbow joint aligned with the motor axis and with initial position equal to 90° . The torque motor delivered perturbations consisting of a pseudo-random binary sequence (Davies, 1970; O'Leary and Honrubia, 1975; Dufresne et al., 1978) of torque pulses $8N-m$ in amplitude. Sixth order m -sequences with 63 elements were used, the duration of each element being 20 ms. Each sequence consisted of trains of flexion and extension pulses whose duration was randomly varied from 20 to 140 ms in integer multiples of 20 ms. The sequence was iterated about 2.5 times so as to span the 3.2 s epoch of each trial. A constant torque equal and opposite to the gravitational torque on the forearm in the horizontal position was added.

Biceps and triceps EMG activities were recorded by means of surface electrodes and forearm angular position was measured by a potentiometer.

Motor Tasks

In the experiments of viscoelastic loading three tasks were examined. In the first the subjects were instructed not to resist the perturbations by remaining as relaxed as possible throughout the trial. The instruction for the second task was to apply a moderate amount of force without attempting, however, to control the perturbed position of their forearm. In the third task, the subjects were instructed to resist the perturbations so as to arrest the forearm oscillations.

In the experiments in which pseudo-random perturbations were used, the subjects were instructed not to resist the applied perturbations initially, but to begin to resist them as quickly as possible upon hearing a command. The command signal was presented with a fixed delay of about one second following the onset of the perturbations. To preclude the subjects from using other cues, the signal was presented in only two thirds of the trials, control trials being randomly interspersed. In the same subjects we also examined the opposite motor task, that is the transition from "resist" to "do not resist" the perturbations.

Data Analysis

The transient responses of the forearm to the viscoelastic perturbations were analyzed both in the time domain and in the frequency domain. We assumed that the responses can be described by a linear second-order model (Viviani and Terzuolo, 1973; Viviani and Berthoz, 1975; Viviani et al., 1976; Agarwal and Gottlieb, 1977; Zahalak and Heyman, 1979):

$$J\ddot{\theta} + C\dot{\theta} + K\theta = 0, \quad (1)$$

where J is the moment of inertia, C is the viscosity coefficient, K is the stiffness coefficient, and θ is the elbow angular position. If $4KJ > C^2$ and the initial conditions are $\theta(0)=1$, $\dot{\theta}(0)=0$ (as in our experiment), then the solution of (1) is:

$$\theta(t) = \exp(-t/\tau)(\cos\omega_d t + (1/\omega_d\tau)\sin\omega_d t), \quad (2)$$

where τ is the time constant of the exponential envelope of the transient response ($\tau=2J/C$), and ω_d is the damped frequency of the oscillations ($\omega_d^2=K/J - C^2/4J^2$). Thus, by measuring the average ω_d and τ of the experimental oscillations, the mechanical parameters of the whole system (forearm+lever+springs) could be determined. The moment of inertia of the forearm was calculated on the basis of the anthropometric tables of Evans (1961). The parameters of the spring-lever complex were evaluated by oscillating it alone. Finally, K and C for the forearm were calculated by subtracting the coefficients of the passive system from those of the whole system.

A frequency-domain analysis of the position data was also performed by means of the Fast-Fourier transform. The parameters K and C were then also determined from the best least-squares fitting of the transformed data. Since the coefficients obtained from the frequency-domain analysis did not differ substantially from those obtained from the time-domain analysis, under Results we shall present only the latter.

In the case of the transitions between “do not resist” and “resist” states, the identification of the impulse response functions of the time-varying system was carried out according to the following procedure (see Soechting et al., 1981 for the complete derivation). If the input $x(t)$ to the system consists of a pseudo-random binary sequence (Davies, 1970; O’Leary and Honrubia, 1975; Dufresne et al., 1978; Marmarelis, 1979) of length N ($N=2^n-1$, where n is the order of the sequence), the output $y(t)$ can be related to the input by means of the impulse response $h(t, \tau)$ through the discrete version of the convolution integral:

$$y(t_j) = \sum_{k=1}^N h(t_j, t_k) x(t_j - t_k), \quad (3)$$

where $t_k = (k-1)\Delta t$, Δt being the interval over which each element of the sequence is defined.

A set of N responses y_i to a set of inputs x_i is obtained, the input sequences x_i being mutually related to a fundamental sequence X by

$$x_i(t_k) = X(t_k + t_i). \quad (4)$$

In other words, in each successive trial the sequence is shifted by one element.

We define the cross-correlation $R_{xy}(t_j, t_m)$ by summing over trials

$$R_{xy}(t_j, t_m) = \sum_{i=1}^N y_i(t_j) x_i(t_j - t_m) \quad (5)$$

and, using (4) and the properties of pseudo-random binary sequences, we obtain

$$h(t_j, t_m) = R_{xy}(t_j, t_m)/(N+1) + \sum_{k=1}^N R_{xy}(t_j, t_k)/(N+1). \quad (6)$$

Physically, the kernel $h(t_j, t_m)$ corresponds to the response at time t_j to a pulse applied at time $t_j - t_m$.

In order to quantify the rate of change of several parameters $w(t)$ of the system, we fitted exponentials of the form

$$w(t) = A(1 - \exp(-kt)) \quad t \geq t' \\ = 0 \quad t < t' \quad (7)$$

for the transition from “do not resist” to “resist”, and:

$$w(t) = A \exp(-kt) \quad t \geq t' \\ = 0 \quad t < t' \quad (8)$$

for the opposite transition. Thus, stiffness and viscosity coefficients were calculated by fitting (1) to the experimental position impulse responses, where K and C in (1) were let vary according to (7) or (8) and the best fit was found by means of a least-squares procedure. A measure of the amplitude of EMG impulse responses was obtained by calculating their maximum deviation from a baseline over the first 100 ms. The baseline was taken to be the mean level of the impulse response for the first 20 ms. The rates of change of the EMG activity were once again calculated according to (7) or (8). From these rates of change, the time courses of the changes in muscular tension attributable to myotatic responses and to overall EMG activity were calculated in the following way. Muscular tension was assumed to be related to EMG through a second order transfer function (Mannard and Stein, 1973):

$$\frac{\text{Tension}(s)}{\text{EMG}(s)} = \frac{M}{(s+b)^2} \quad (9)$$

with $b = 5\pi$ (Soechting and Roberts, 1975). The convolution of $\text{EMG}(t)$ (defined by Eq. 7) with the anti-transform of the transfer function defined by (9) gives for the transition from “do not resist” to “resist” [assuming $t' = 0$ in (7)]:

$$\text{Tension}(t) = MA \int_0^t (1 - \exp(-k\alpha)(t-\alpha) \exp(-b(t-\alpha))) d\alpha \quad (10)$$

which becomes:

$$\text{Tension}(t) = MA/b^2 [(1 - \exp(-bt)) - bt \exp(-bt)] \\ - MA \exp(-kt)/(k-b)^2 [(1 - \exp((k-b)t)) \\ + (k-b)t \exp((k-b)t)]. \quad (11)$$

For the transition from “resist” to “do not resist” we obtain:

$$\text{Tension}(t) = MA \int_{-\infty}^t (t-\alpha) \exp(-b(t-\alpha)) d\alpha \\ + MA \int_0^t \exp(-k\alpha)(t-\alpha) \\ \cdot \exp(-b(t-\alpha)) d\alpha \quad (12)$$

which becomes:

$$\text{Tension}(t) = MA/b^2 [(1 + bt) \exp(-bt)] \\ + MA \exp(-kt)/(k-b)^2 [(1 - \exp((k-b)t)) \\ + (k-b)t \exp((k-b)t)]. \quad (13)$$

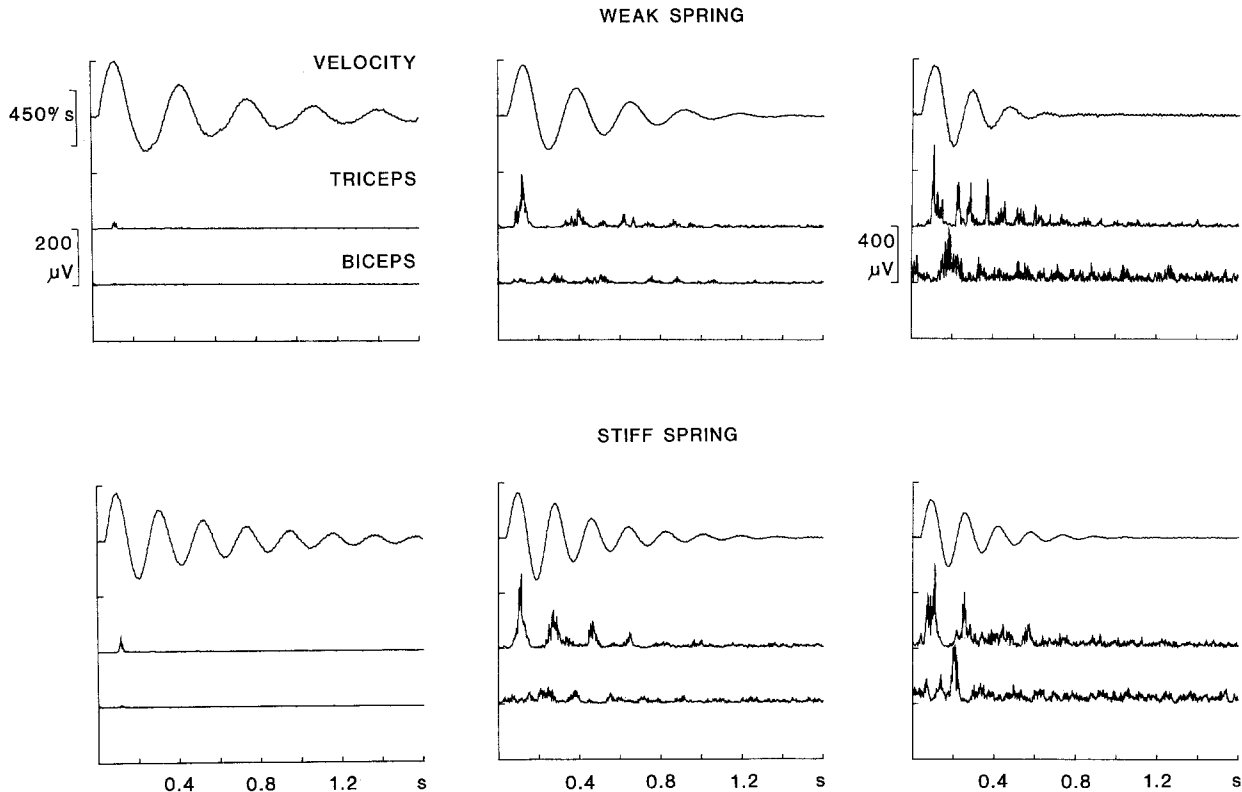


Fig. 1. Viscoelastic loading with weak and stiff springs. The first trace in each panel corresponds to forearm angular velocity (flexion is upwards). The second and third traces are rectified EMG activities of triceps and biceps, respectively. The first column corresponds to the task "do not resist", the second column to the task "apply a small force", and the third one to the task "resist maximally". The calibrations for all panels are on the left-hand side of the figure, except for the EMG activities of the top right panel. In all conditions, the forearm initial position was about 110° elbow extension and the maximal excursion induced by the perturbations was to about 65° elbow flexion

Results

Viscoelastic Loading

This first series of experiments was performed to determine how effectively the human forearm compensates for a large mechanical perturbation at different operating points. The effectiveness can be judged by evaluating various parameters of the transient response (such as its peak amplitude, time to peak, settling time etc.) which depend on the values of the elastic and viscous components of impedance.

Figure 1 shows results from one experiment in which the forearm was loaded viscoelastically with either the weak spring or the stiff one. Averages of five trials are shown in each panel: the top traces correspond to the elbow angular velocity, the two lower traces to the rectified EMG of triceps and biceps. The first column corresponds to the task "do not resist the perturbations", while the second column corresponds to the task "apply a small force", and the third to the task "resist the perturbations so as to arrest the movement". The first general observation is that the frequency of the forearm oscillations increases as more muscular activity is produced by the subject and that

the oscillations are damped out more rapidly. Thus, the stiffness and viscosity of the forearm are larger in the tasks involving active resistance of the perturbations relative to their values during the "do not resist" task. We shall now examine these results in more detail.

The amount and pattern of EMG activity change considerably according to the instruction given the subject. When he is asked not to resist the perturbations, there is just one small burst in triceps concomitant with the first large peak of angular velocity in the flexor direction. When the subject is intentionally applying some force, EMG activity increases substantially: triceps and biceps are now reciprocally organized and they burst in coincidence with the velocity peaks of their stretching and pause during unloading (Terzuolo et al., 1974). Finally, when the subject is asked to resist the perturbations so as to arrest the movement, EMG amplitude increases even further and its modulation in phase with velocity now occurs over an appreciable background level.

The changes in the transient response of the forearm to the applied perturbation parallel those in muscular activities. They can be appreciated from Figs.

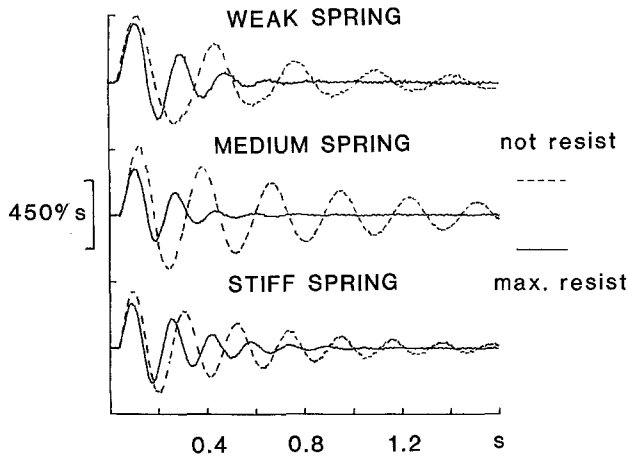


Fig. 2. Comparison of forearm velocity responses during the tasks “do not resist” and “resist maximally”. Data are from the same experiment as Fig. 1. Note the increase in frequency and the decrease in settling time of the oscillations when the subject resists the perturbations

1 and 2; the latter shows (for the same experiment as Fig. 1) the velocity responses for the “do not resist” and “maximally resist” conditions superimposed for all three elastic loads. Note that the greater is the mean level of muscular tension, the shorter is the duration of the oscillations induced by the disturbance. Whereas the oscillations are still appreciable after 1.6 s when the subject does not resist, they are damped out after 0.8–1 s when he is actively opposing them. On the contrary, the amplitude of the first maximum and minimum of the velocity curves changes much less. With the weak and stiff springs, in particular, the amplitude has decreased by only 10–20% at “maximally resist” relative to its value at “do not resist”.

These changes in forearm mechanical impedance with the tasks were quantified by fitting (1) to the data (see Methods). The average of the values for the stiffness (K) and viscosity (C) over all the subjects are reported in Table 1. If we consider the average of the results obtained with all three springs, we see that in

the “maximally resist” condition the stiffness coefficient (K) is more than five times as great, and the viscosity coefficient (C) is about four times as great as their respective values in the “do not resist” condition. Correspondingly, the damping ratio ($\xi = (C^2/4JK)^{1/2}$) does not change greatly, the natural frequency ($\omega_n = (K/J)^{1/2}$) changes proportionately to the square root of stiffness, and the settling time (defined as the time after which the oscillations remain within 2% of final position, $T_s = 8J/C$) undergoes a fourfold variation. Assuming the system is linear so that the present results can be extended to different inputs, the fact that ξ does not modify considerably, while T_s does, means that the main effect of an increase in muscular activity upon the forearm transient response to a step input would consist not so much in an attenuation of the percentage of overshoot of the initial displacement as in a greatly reduced duration of the induced oscillations.

In fitting (1) to the data we assumed that the system is stationary over the duration of each trial and therefore K and C in (1) should be constant for each task. However, the time constant τ of the exponential envelope of the forearm transient response changes during the trial when the subject is actively resisting the perturbations. τ is significantly longer during the first period of the oscillations than afterwards. Since $\tau = 2J/C$, this observation implies that, (assuming a linear system) the increment in viscosity of the forearm system takes time to build up when the subject is resisting the perturbations. For instance, in the case of “maximally resist” with the stiff spring, C is equal to 0.45 $N\text{-m-s/rad}$ over the first period, 0.85 over the second, 1.07 over the third, and 1.32 over the fourth (that is at more than 500 ms after the beginning of the perturbations).

Pseudo-Random Perturbations

We have just seen that when the task involves an active resistance of large viscoelastic disturbances, the fore-

Table 1. Mechanical parameters of forearm transient responses to viscoelastic loads. The values obtained for all the subjects have been averaged. K is stiffness coefficient, C is viscosity coefficient, ξ is the damping ratio, ω_n is the natural frequency, and T_s is the settling time within 2% of final position. In the “maximally resist” condition the parameters were not constant throughout the trial (see text), and thus the table reports the mean values over the trial

Spring	Do not resist					Resist					Maximally resist				
	K ($N\text{-m/rad}$)	C ($N\text{-m-s/rad}$)	ξ	ω_n (rad/s)	T_s (s)	K ($N\text{-m/rad}$)	C ($N\text{-m-s/rad}$)	ξ	ω_n (rad/s)	T_s (s)	K ($N\text{-m/rad}$)	C ($N\text{-m-s/rad}$)	ξ	ω_n (rad/s)	T_s (s)
Weak	15.1	0.39	0.142	5.5	2.56	42.5	0.91	0.197	9.2	1.10	125.5	1.24	0.157	15.8	0.81
Medium	14.8	0.22	0.081	5.4	4.55	43.0	0.70	0.151	9.3	1.43	114.0	1.56	0.207	15.1	0.64
Stiff	33.3	0.33	0.081	8.2	3.03	44.9	0.31	0.065	9.5	3.23	111.9	1.08	0.144	15.0	0.93
Mean	21.1	0.31	0.101	6.4	3.38	43.5	0.64	0.138	9.3	1.92	117.1	1.29	0.169	15.3	0.79

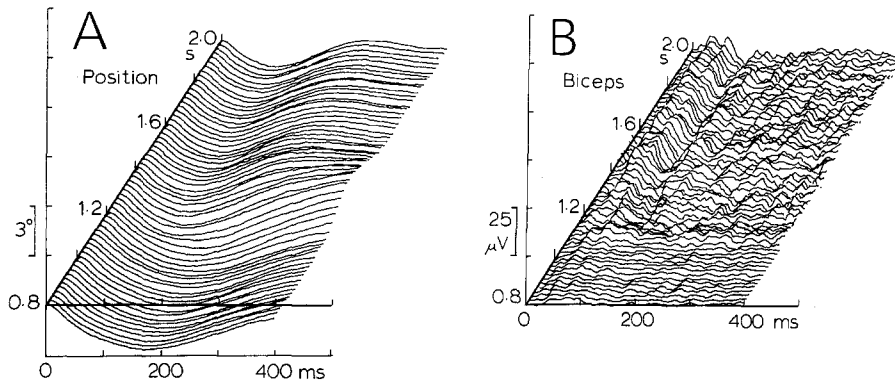


Fig. 3A and B. Transient responses to pseudo-random perturbations. The impulse responses of position and biceps EMG are plotted in **A** and **B**, respectively, for the transition from “do not resist” to “resist”. Each trace depicts the impulse responses at the time indicated by the oblique scale, time being measured from the onset of the perturbations. As plotted, they represent the average contribution to the output by a pulse tending to extend the forearm and occurring 0–400 ms before. The signal to resist was given at 1 s

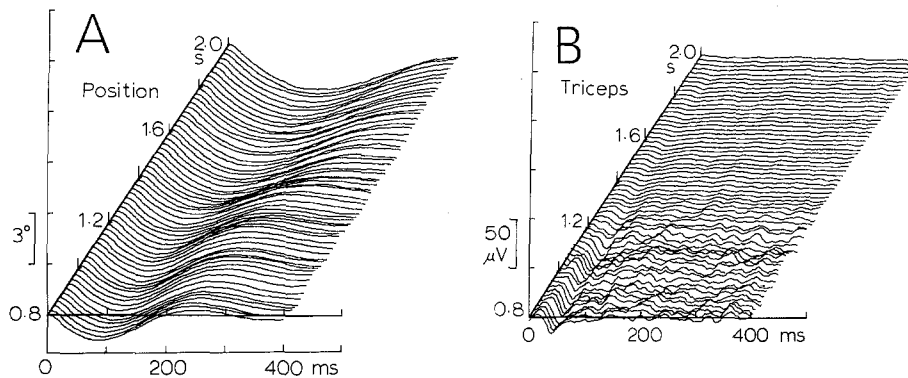


Fig. 4A and B. Impulse responses of position and triceps EMG during the transition from “resist” to “do not resist”

arm oscillations are damped out more effectively than when the subject remains passive, but that it may take an appreciable time for the mechanical impedance to build up to its final value. Such results prompt the following question: What is the time course of the changes in output impedance in the transition between the two operating points defined by the “do not resist” and “resist” instructions? In order to address this question we performed a second series of experiments where the applied perturbations consisted of small pseudo-random torque pulses, and the instruction given the subject was not to resist the perturbations initially but to begin to resist them as quickly as possible upon hearing a signal. We previously showed (Soechting et al., 1981) that such a task is accomplished by a fast and powerful co-activation of biceps and triceps. It was also found that the amplitude of the myotatic responses starts to increase in both muscles at the same time as does overall EMG activity. However, the time course of the modulation of the former is slower than that of the latter. Since both reflex and intentional activations of the forearm muscles affect the limb mechanical impedance, it is interesting to compare the time course of the latter with that of each one of the former.

Figure 3 shows the impulse responses of forearm position (Part A) and biceps EMG activity (B) from

one such experiment. They have been calculated according to (6). The oblique axis represents time (t_j) measured from the onset of the trial. Each plotted trace represents the impulse response at t_j to a 20 ms pulse of torque tending to extend the forearm. They denote the average contribution to position or biceps EMG at time t_j by a pulse occurring 0–400 ms prior to t_j (that is at $t_j - t_m$). From Fig. 3A one can see that the forearm transient response changes substantially in the transition between the two operating points. Initially, when the subject is not resisting the perturbations, the maximum average displacement produced by the torque pulse is about 3° and has a time to peak of about 200 ms. At $t_j = 1$ s the command signal is presented and, after a reaction time of 120 ms, the subject starts to co-contract his forearm muscles. Correspondingly, and after a further delay due to inertia, the impulse responses of position change in amplitude and frequency: the former decreases and the latter increases, so that the oscillations are damped out more rapidly than before. In the stationary condition of active resisting, peak amplitude and time to peak have decreased to about 50–60% of their initial value. Figure 4A shows the opposite trend during the transition from “resist” to “do not resist”. The changes in forearm transient responses to small perturbations indicate that the mechanical parameters of the system

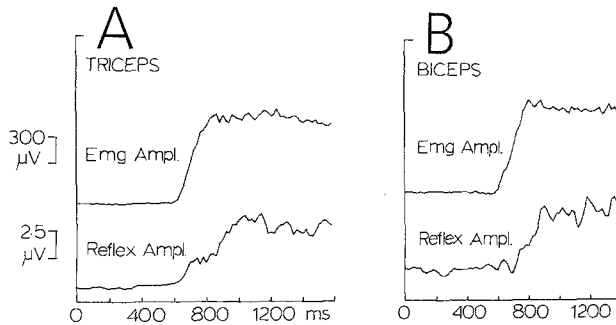


Fig. 5A and B. Time course of the changes in the amplitude of overall EMG activity (top traces) and those of the myotatic response (lower traces) during the transition from “do not resist” to “resist”. The data from all the subjects have been averaged. The baseline for myotatic response amplitude corresponds to the time scale. The signal for the transition was presented at $t=500$ ms on this time scale. Note the slow time course of the changes in the reflex amplitude

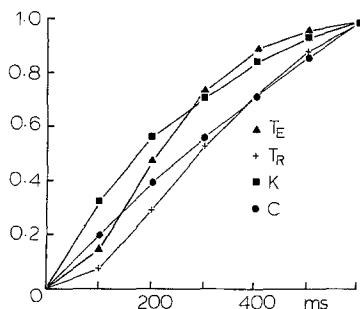


Fig. 6. Time course of the changes in tension, stiffness and viscosity during the transition from “do not resist” to “resist”. The curve labelled T_e corresponds to the changes in tension attributable to overall EMG activity, T_r to those attributable to the myotatic response; K corresponds to the changes in stiffness coefficient and C to those in viscosity coefficient of the second-order mechanical model. The data have been normalized under the assumption that the changes in all parameters begin and end at the same time

also change as a function of the operating point. Before considering such changes quantitatively and examining their time course, we shall comment briefly upon the changes in the myotatic responses and overall EMG activity (a complete account is given in Soechting et al., 1981).

Figure 3B shows that the amplitude of the myotatic response is rather small initially, when the subject is not resisting the perturbations, but that it increases as he starts to resist. The time course of such changes, as well as that of overall EMG activity, is shown in Fig. 5A for triceps and in Fig. 5B for biceps. The data from all subjects have been averaged. The upper traces depict the temporal modulation of the amplitude of overall EMG activity, calculated as the average of full-wave rectified EMG activity of all the trials and comprising therefore both activity uncorrelated with the perturbations as well as activity correlated with

Table 2. Time constants of the changes in tension, stiffness and viscosity in the transition from “do not resist” to “resist” the pseudo-random perturbations (left half) and in the opposite transition (right half). The time courses of biceps and triceps have been averaged. μ_t corresponds to the contribution to tension by overall EMG activity, μ_r to that by myotatic responses; μ_k corresponds to the stiffness coefficient and μ_c to the viscosity coefficient. All values are in seconds

Experiment	Do not resist \rightarrow Resist				Resist \rightarrow Do not resist			
	μ_t	μ_r	μ_k	μ_c	μ_t	μ_r	μ_k	μ_c
1	0.20	0.28	0.23	0.28	0.22	0.26	0.06	0.20
2	0.29	0.32	0.20	0.32	0.28	0.28	0.13	0.30
3	0.27	0.35	0.24	0.34	0.27	0.30	0.18	0.28
4	0.25	0.34	0.28	0.34	0.23	0.28	0.12	0.32
Mean	0.25	0.32	0.24	0.32	0.25	0.28	0.12	0.28

them. The lower traces depict the changes in EMG impulse response amplitude evaluated over the first 100 ms of t_m (see Methods). It is evident that the rate of increase of the myotatic response amplitude is considerably slower than that of overall EMG activity. In order to make a comparison with the time course of changes in mechanical impedance, it is more appropriate to consider the time course of the changes in muscular tension. They have been calculated according to the procedure described under Methods. If the changes in EMG amplitude follow an exponential course [Eqs. (7) or (8)], then the profile of tension changes during the transitions is sigmoidal [and is described by Eqs. (11) or (13)]. Figure 6 shows such profiles for one representative experiment, together with the estimated changes in stiffness and viscosity (see below). T_e corresponds to the changes in tension attributable to overall EMG activity, T_r to those attributable to the myotatic response. The data have been plotted on a normalized scale under the assumption that the steady-state values of all parameters are reached 600 ms after the beginning of the transition. We calculated as an equivalent of a time constant the time when tension is $(1 - 1/e)$ of its value at 600 ms for the transition from “do not resist” to “resist”, and the time when it is $1/e$ of its final value for the opposite transition. Such times are listed in the first two columns of Table 2, μ_t corresponding to the contribution to tension by overall EMG activity, and μ_r corresponding to the contribution by myotatic responses. Obviously, as the time course of changes in myotatic response amplitude is lower than that in overall EMG activity, so is the time course of changes in tension due to the former relative to the time course of tension changes due to the latter.

The time course of the changes in forearm stiffness and viscosity was instead evaluated by fitting to the

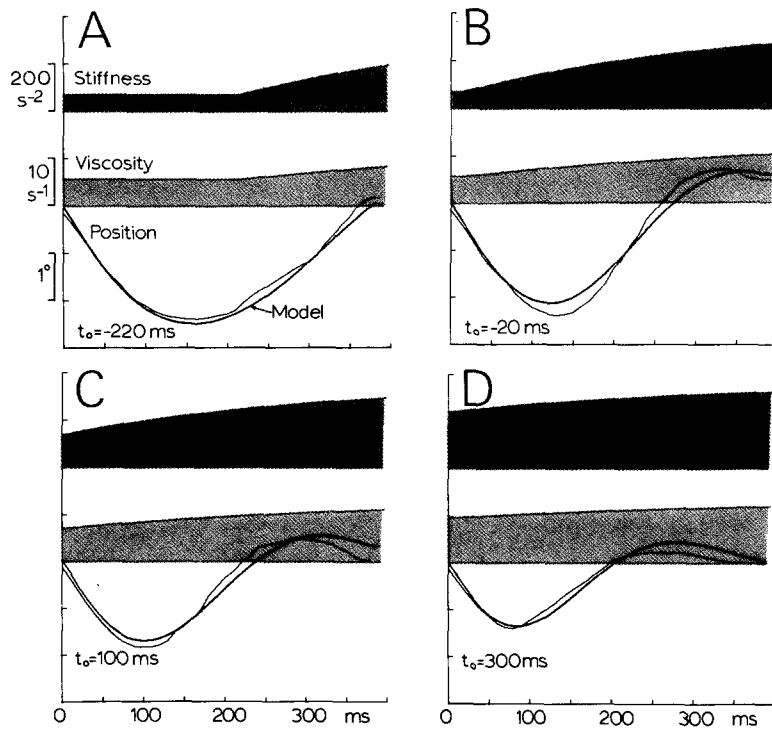


Fig. 7A–D. Fitting of the mechanical model to the forearm position responses for the transition from “do not resist” to “resist” the pseudo-random perturbations. In the lower part of each panel the experimental position response (thin line) to a pulse applied at $t=0$ and the model (thick line) are plotted versus time. In the upper part of the panels are plotted the temporal changes in stiffness and viscosity coefficients (more precisely, K/J and C/J , respectively) corresponding to the model. The four panels correspond to four different times t_0 relative to the onset of the transition

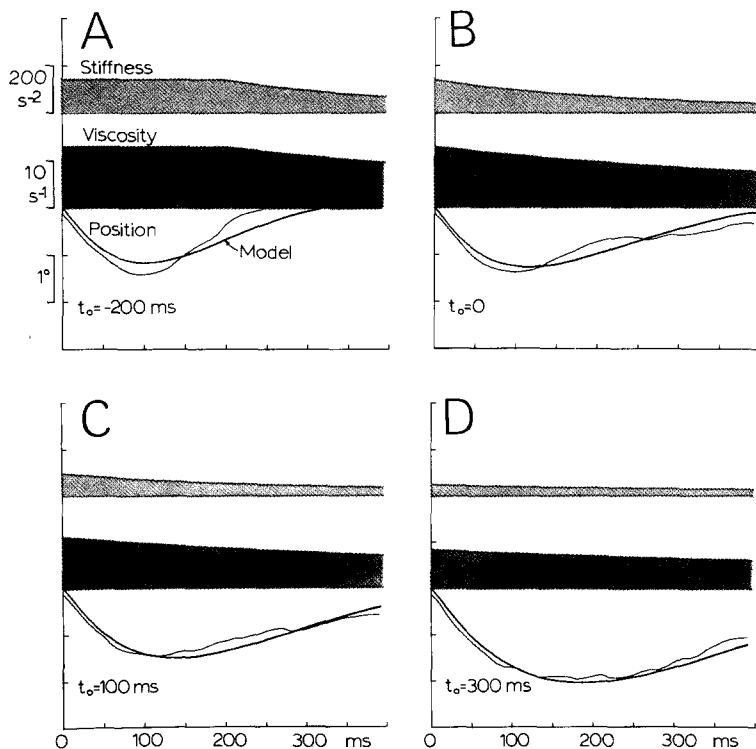


Fig. 8A–D. Mechanical model for the transition from “resist” to “do not resist”

position impulse responses a second-order model whose parameters K and C were let vary as exponential functions of t_j (see Methods). Figure 7 shows the results of such fitting for the transition from “do not resist” to “resist”, and Fig. 8 for the transition in the opposite direction. In the lower part of each panel the experimental position response (thin line) and the

model (thick line) are plotted versus time. The four panels in each figure depict the changes in position produced by a pulse occurring at four different times t_0 measured relative to the onset of the transition. The model appears to be adequate to reproduce the experimental data; it tends, however, to overestimate the damping ratio in Figs. 7B and Fig. 8A. In the upper

Table 3. Steady-state values of forearm mechanical parameters obtained with pseudo-random perturbations

Experiment	Do not resist					→	Resist				
	K ($N-m/\text{rad}$)	C ($N-m-s/\text{rad}$)	ξ	ω_n (rad/s)	T_s (s)		K ($N-m/\text{rad}$)	C ($N-m-s/\text{rad}$)	ξ	ω_n (rad/s)	T_s (s)
1	13.9	1.17	0.347	8.2	1.40		61.9	2.11	0.296	17.4	0.78
2	5.5	0.66	0.311	5.2	2.48		36.6	1.05	0.192	13.4	1.56
3	16.6	1.74	0.472	9.0	0.94		79.5	1.93	0.239	19.7	0.85
4	19.1	0.88	0.222	9.7	1.86		70.5	1.11	0.146	18.5	1.48
Mean	13.8	1.11	0.338	8.0	1.67		62.1	1.55	0.218	17.3	1.17

Experiment	Do not resist					←	Resist				
	K ($N-m/\text{rad}$)	C ($N-m-s/\text{rad}$)	ξ	ω_n (rad/s)	T_s (s)		K ($N-m/\text{rad}$)	C ($N-m-s/\text{rad}$)	ξ	ω_n (rad/s)	T_s (s)
1	9.6	0.97	0.346	6.8	1.69		38.1	2.42	0.433	13.6	0.68
2	16.3	2.05	0.561	8.9	0.80		70.9	3.63	0.476	18.6	0.45
3	6.4	1.34	0.585	5.6	1.22		30.1	2.67	0.537	12.1	0.61
4	13.7	1.38	0.412	8.2	1.19		48.6	2.17	0.344	15.4	0.76
Mean	11.5	1.44	0.476	7.4	1.23		46.9	2.72	0.448	14.9	0.63

part of each panel we have plotted the changes in stiffness and viscosity coefficients (more precisely, K/J and C/J) corresponding to the model. The time course of the change in stiffness is faster than that of viscosity, both in Figs. 7 and 8. These time courses are also shown in Fig. 6, the curve labelled K corresponding to the changes in stiffness coefficient, the curve labelled C to the changes in viscosity coefficient. The third and fourth columns of Table 2 report the time constants for the former (μ_k) and for the latter (μ_c), respectively, calculated in the same manner as those for T_e and T_r .

Table 3 gives the steady-state values of K , C , ξ , ω_n , and T_s for the transition from “do not resist” (upper half) and for the opposite transition (lower half). In the “resist” condition K is more than four times as great and C is about one and half times as great as their respective values in the “do not resist” condition. Correspondingly, when the subject resists the perturbations, ξ tends to be smaller whereas T_s becomes one half times as short as it is in the “do not resist” state.

Discussion

Two main results have emerged from both experimental approaches. First, when a subject actively resists applied perturbations both the equivalent stiffness and viscosity of the forearm are greater than when he does not. Secondly, the changes in mechanical impedance

associated with the transition between the two conditions develop with a relatively slow time course.

The fact that the mechanical parameters of the forearm do vary according to the task is already evident from inspection of the transient responses to both the large viscoelastic perturbations and the small pseudo-random torque pulses. When the subject opposes the perturbations, the frequency of the oscillations is higher and these are damped out more rapidly than when he is not resisting. By assuming a simple linear second-order model, we calculated the coefficients of virtual stiffness (K) and viscosity (C) for the whole system. The steady-state values of K and C so obtained for the viscoelastic loading are in substantial agreement with those obtained for the pseudo-random perturbations, and are also comparable with those reported in other studies involving similar conditions (Soechting et al., 1971; Zahalak and Heyman, 1979). Viviani et al. (1976) investigating intentional sinusoidal movements of the forearm found an average K which falls in the range of our values; the viscosity coefficient was instead twice as large as the largest value obtained in the present research. Both K and C reported by Viviani and Terzuolo (1973) are substantially larger than the values we obtained, but the task they examined required the production of much larger forces (maximal acceleration and arrest of a ballistic movement).

The observed dependence of the steady-state values of mechanical impedance upon the task may be ac-

counted for by the fact that, when the subject resists the perturbations, both the mean level of EMG activity and the amplitude of the myotatic response are greater than when he does not. On this subject, the notion that the elastic and viscous components of stiffness depend in a roughly proportional manner upon the mean muscular tension is well established in the literature (Buchthal and Kaiser, 1944; Wilkie, 1950; Stark, 1968; Joyce and Rack, 1969; Houk et al., 1970; Rosenthal et al., 1970; Agarwal and Gottlieb, 1977; Zahalak and Heyman, 1979). The number of viscoelastic elements of the muscle (or muscles) engaged by the stretch input increases, in fact, with the level of contraction, and it has been suggested that both tension and stiffness have their source in cross-bridge formation (Huxley and Simmons, 1972). Also, the observation that the amplitude of myotatic responses is an increasing function of the intensity of contraction is well established (Marsden et al., 1972; Dufresne et al., 1978; Soechting et al., 1981). Moreover, the present data show that, if one assumes that the input to the stretch reflex is represented by angular position and its derivatives (Dufresne et al., 1978, 1979), the increase in amplitude of the myotatic responses reflects in fact an increase in the gain of the feedback loops, and thus in their contribution to the overall impedance.

Whereas the recognition of the importance of both reflex and intrinsic muscular actions in the genesis of overall impedance is general, the evaluation of their individual relative contributions at different operating points is instead a matter of considerable controversy in the literature (cf. Granit, 1970; Matthews, 1972; Stein, 1974; Houk, 1978; Terzuolo et al., 1981). For example, several authors have argued on different grounds that the stiffness of the reflex loop is low and, consequently, its load-compensating capabilities are rather poor (e.g. Vallbo, 1974; Bizzi et al., 1978). Our data do not readily permit the separate identification of reflex and muscular contributions to output impedance, but they do give evidence of the existence of limits in the performance of the overall system under the present experimental conditions.

The effectiveness of the motor system in compensating for a disturbance is often evaluated in terms of its steady-state performance (cf. Houk, 1978). A steady-state error may be defined as the final deviation from the initial or reference position. If the system is second-order [see Eq. (1)] and the input is a unit step function, then the steady-state error depends exclusively on the stiffness coefficient K , being simply equal to $1/K$. Thus, the substantial increase in K we observed when the subject resisted the applied perturbations implies that the steady-state error to a step

input would have decreased correspondingly. The steady-state error, however, does not characterize completely the performance of a system which has to deal with external disturbances. In certain behavioral situations, it may be important for the system to minimize not so much the steady-state error as the transient oscillations induced by the disturbance and the time required to reach a steady-state. An increase only in the stiffness, in that case, would be detrimental (the damping ratio is inversely proportional to the square root of K). In fact, it would be more advantageous to have a relatively compliant resistance, but a large viscosity.

Since the tasks we investigated did not require an accurate control of the final position, a minimization of the steady-state error was not implied. Indeed, in the experiments involving viscoelastic loading, the final position was forced towards the equilibrium point of the springs acting on the forearm. Also, in the experiments involving pseudo-random perturbations, no instruction was given regarding the final forearm position. Instead, the tasks emphasized the minimization of the transitory displacements caused by the disturbance. Nevertheless, we consistently found that the increment in stiffness associated with the task of opposing the perturbations is greater than that in viscosity and, as a consequence, the damping ratio does not modify substantially relatively to its value in the "do not resist" condition. (However, the settling time, which depends on the viscosity coefficient, does become shorter.) This observation agrees with the results reported by Stark (1968) for free-wheeling wrist pronation-supination movements executed with different intensities of contraction, and by Agarwal and Gottlieb (1977) for a task involving the resistance of random torque perturbations of the ankle joint superimposed on different values of constant bias torque.

Temporal variations in the impedance have not been described previously. On this subject our results showed that not only does stiffness change to a greater degree, but it also changes faster than viscosity in the transition between the "do not resist" and "resist" states. In particular, when the subjects were asked to oppose the viscoelastic loads, they rapidly produced a much larger level of EMG activity than that present in the passive condition; nevertheless the forearm viscosity built up rather slowly. Similarly, when the subjects were asked to switch as quickly as possible between the task of not resisting the pseudo-random perturbations and that of opposing them, the time constants of the changes in the stiffness and viscosity coefficients were longer than 200 ms. Furthermore, in this latter case we consistently found that the changes

in viscosity lag behind those in stiffness as well as those in the contribution to tension due to overall EMG activity.

Since the mechanical model of the forearm which we used in order to calculate stiffness and viscosity coefficients is an equivalent, lumped-parameter one, it is impossible to assign any direct and unique physical counterpart to its parameters. Thus, the relative sluggishness in the changes of mechanical impedance may well have both a muscular substratum and a neural one. However, on the basis of the relative parallelism between the time course of the changes in viscosity and that in the tension contributed by the myotatic response (Fig. 6), one may hypothesize a significant participation of reflex mechanisms in the genesis of dynamic impedance. This observation would also agree with the data presented by Viviani and Terzuolo (1973) who modelled ballistically initiated movements which had to be arrested as quickly as possible, by introducing a delayed viscosity term representing the reflex contribution, which could amount up to 75% of the total torque produced by the forearm in their experimental condition.

If such a reflex contribution to forearm impedance is accepted, it becomes possible to account for the finding that the changes in myotatic response amplitude associated with tracking tasks involving a very accurate control of the instantaneous position are fast and always lead those in overall EMG activity (Dufresne et al., 1980; Gottlieb and Agarwal, 1980; Soechting et al., 1981). In fact, as the time course of reflex changes is highly task-dependent, so could be that of mechanical impedance, and such an adaptive behavior would probable represent the real strength of the system.

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